

seven species of *Engelhardia*, the one species of *Platycarya*, 14 species of *Carya*, seven species of *Pterocarya*, and 16 species of *Juglans*. Several varieties of some species were studied. In general, from one to three collections were obtained for each species. More detailed studies of pollen size and pore number variation in several taxa have been carried out and discussed in a previous paper (Whitehead, 1963).

The author wishes to express his thanks to Dr. Elso S. Barghoorn who first suggested the study and gave many valuable suggestions and to Dr. Cortez Hoskins for his helpful comments on a preliminary draft of the manuscript. The writer is especially indebted to the directors of the Arnold Arboretum (A) and the Gray Herbarium (GH) for permission to collect staminate material. Additional collections were provided by Dr. Wayne E. Manning and Dr. Donald E. Stone. Slides available in the reference collection of the Geological Survey of Denmark (DGU) were studied as well. The Jersey Production Research Company kindly granted permission to publish the results of the investigation, part of which was carried out while the writer was employed as a consultant. The author is deeply grateful to Dr. Johannes Iversen and his colleagues of the Geological Survey of Denmark for permission to use the facilities of their institute and for many stimulating discussions concerning the paper. Special thanks are due to Drs. Stone and Manning for their extraordinarily careful criticism of the penultimate draft of the manuscript. Support for the final phase of the project has been provided by Grant G-17277 from the National Science Foundation.

METHODS

Whole mounts of pollen grains were prepared as outlined previously (Whitehead, 1963; treatment with KOH, acetolysis, and mounting in silicone oil). Choice of techniques was predicated on the considerations discussed by Christensen (1946), Andersen (1960), and Whitehead (1962, 1964).

Pollen size measurements for *Carya*, *Juglans*, and *Pterocarya* were carried out with a high-dry objective (ocular interval = 2.04 micra). Measurements for *Alfaroa*, *Engelhardia*, and *Platycarya* were made with oil immersion (ocular interval = 0.82 micra). Fifty measurements were obtained for each collection. Pore number and frequency of heteropolar grains were noted for *Juglans* and *Pterocarya*.

Of the slides available in the pollen reference collection of the Geological Survey of Denmark, only preparations in silicone oil or Tangelfoot medium were selected for study (grains mounted in Tangelfoot are identical in size to those mounted in silicone oil (Andersen, 1960)). Supplementary data on *Carya* and *Juglans* have been obtained through the courtesy of Dr. Svend Th. Andersen, who, in collaboration with Dr. Stanley A. Cain, has accumulated a number of observations on the North American species of these genera. Andersen and Cain's data were derived from pollen prepared by acetolysis (2 minutes) and mounted in glycerine-

jelly (Andersen, personal communication), hence direct size comparisons must be made with caution. However, the nearly perfect concordance of these data with those obtained by the author (see TABLE 4) suggests that the measurements from glycerine-jelly preparations may be divided by 1.06 for direct comparison. This corresponds to the correction factor of 1.15 determined by Faegri and Iversen (1964, pages 169-170).

THE PROBLEM OF POLLEN SIZE

It is evident that a variety of factors, both genetic and environmental, operate in concert to influence the size of modern pollen grains. It then follows that to obtain meaningful data on pollen size one must accumulate measurements from a number of collections distributed over the geographic range of the species and encompassing the diversity of ecological situations in which it occurs. This also will help minimize the effects of climatically aberrant years. As some of the pollen size data presented in this study involve only one or two collections, they must be considered preliminary and not necessarily characteristic for the particular species. The same reservation applies to the data on pore number for *Juglans* and *Pterocarya*.

The size data presented in this investigation will doubtless be compared with those of Erdtman (1943, 1952), Heimsch (1944), Wodehouse (1935), Stachurska (1961), Stone (1963), and others, thus it is important to note that such comparisons must be made with extreme caution. The studies of Christensen (1946) and Andersen (1960) demonstrate clearly the effect of both chemical treatment and mounting medium on pollen size and indicate that direct comparisons are possible only when identical techniques have been employed. For example, the measurements of Stachurska (1961) are systematically larger than those presented in the present study, as she employed acetolysis and mounted the grains in glycerine-jelly.

It should be emphasized that for size studies a medium in which pollen size is stabilized must be employed. Glycerine-jelly is not to be recommended. The unpredictable swelling of grains in this medium is well known (e.g., Christensen, 1946; Andersen, 1960; Cushing, 1961; Faegri & Deuse, 1960). This is demonstrated by the lack of correspondence between many of Stachurska's measurements (e.g., those for *Carya ovalis*) and those of Andersen and Cain, Stone (1963), and the writer.

The application of size-frequency data from modern pollen to the identification of fossil pollen involves even more complex considerations. Seldom can direct size comparisons be made between modern and fossil grains. The environment of preservation seems to alter the exine of fossil grains chemically so that it does not respond to treatment in the same manner as modern pollen (Christensen, 1946; Buell, 1946). Furthermore, as Andersen (1960) has indicated, pollen grains of a given species differ in size depending upon the type of sediment in which they have been preserved. Grains are apparently smallest in calcareous sediments and largest in more acid types. Consequently, it is often impossible to make

direct size comparisons between fossil grains from different levels of the same core. These various factors must be considered carefully in any application of pollen size data.

POLLEN MORPHOLOGY

Alfaroa

The pollen grains of *Alfaroa* (TEXT-FIGURES 1-6) are tectate, triporate (occasionally with two, four, and five pores), suboblate, subtriangular (rounded triangular) in polar view, and possess a fine, even, scabrate sculpture. The pores are equatorial in position and may be very slightly aspidate. The pore vestibulum is an open, low cone defined by the endexine which stops approximately two to three micra short of the pore aperture (exopore) leaving a low, ill-defined rim (TEXT-FIGURES 3 and 5). The ectexine thickens very slightly at the pore. The pore aperture is 2 to 3 micra in diameter and somewhat variable in shape. According to Erdtman (1952) the exopore is meridionally elongated, while in the collections studied by the writer it was more or less circular.

The ectexine is mostly homogeneous, consisting of a relatively thick tectum and a much reduced columella layer. The extent of the foot layer is not known. Columellae are discernible within the vestibulum, where they are visible in optical section (oil immersion only). They are relatively tightly packed and somewhat irregular in distribution. The pattern is best seen with phase contrast. It is apparent that the ectexinous thickening of vestibulum involves columella layer more than the tectum. Columellae could not be differentiated outside of the vestibulum.

The grains studied varied in size from 18.6 to 28.4 micra, with a mean of 23.5 (TABLE 1). This corresponds well to the sizes reported by Erdtman (1952) and Heimsch (1944). The exine is approximately 1.6 micra thick, of which the endexine (and foot layer?) contributes less than 0.5 micra. The exine appears to be relatively uniform in thickness over the entire surface of the grain (except surrounding the pore) in contrast to *Juglans* and *Carya* in which a distinct thinning of the exine occurs on the proximal pole. The scabrate sculpture, consisting of evenly spaced elements (less than 0.4 micra in diameter) is present over the entire surface of the grain, including the vestibulum. It is probable that the individual sculptural elements are actually micro-echinae (fine spines) comparable to those observed recently with electron microscopy in *Juglans* and *Carya* (Stone *et al.*, 1964).

In the collection of *A. costaricensis* upon which Heimsch (1944) has reported, 66 per cent of the grains were triporate, 34 per cent tetraporate, and less than 1 per cent pentaporate. However, in only one of the collections which the present writer studied (*A. costaricensis* var. *costaricensis*, *Skutch 4684*) were numbers of tetraporate grains encountered and this was clearly an aberrant collection, as the fourth pore was always polar rather than equatorial in position. Diporate and tetraporate grains were extremely rare in the other collections studied.